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RESEARCH ARTICLE

Landscape dynamics of floral resources affect the supply of a biodiversity-dependent cultural ecosystem service

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Abstract
Context Cultural ecosystem services, many of which depend on biodiversity, are recognized as important but seldom quantified biophysically across landscapes. Furthermore, many ecosystem service models are static, and the supply of cultural ecosystem services may be misrepresented if seasonal shifts in biotic communities are ignored.
Objectives We modeled landscape dynamics of wildflower blooms in a temperate montane landscape to determine (1) how floral resources (wildflower species richness, abundance, timing, and presence of charismatic species) changed over the growing season, (2) how projected wildflower viewing hotspots varied over space and time, and (3) how spatial shifts in floral resources affected potential public access to wildflower viewing.
Methods Data were collected at 63 sites across a rural-to-urban gradient in the Southern Appalachian Mountains (USA). Generalized linear models were used to identify factors affecting floral resources at two temporal scales. Floral resources were projected across the landscape and hotspots of wildflower viewing were quantified using overlay analysis.
Results Floral resources were affected by topoedaphic conditions, climate, and surrounding building density and changed seasonally. Seasonal models revealed locational shifts in ecosystem service hotspots, which changed the proportion of hotspots accessible to the public and identified wildflower-viewing opportunities unnoticed by static models.
Conclusion Relationships between landscape gradients, biodiversity, and ecosystem service supply varied seasonally, and our models identified cultural ecosystem service hotspots otherwise obscured by simple proxies. Landscape models of biodiversity-based cultural ecosystem services should include seasonal dynamics of biotic communities to avoid under- or over-emphasizing the importance of particular locations in ecosystem service assessments.

Keywords Cultural services · Ecosystem service capacity · Temporal pattern · Wildflowers · Nature-based recreation

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Introduction

Sustaining the supply of ecosystem services has become a primary goal of landscape management worldwide. Ecosystem services are integral to policies at local, regional and national levels (Millennium Ecosystem Assessment 2005; TEEB 2009), and sustainable management of the supply of ecosystem services depends on understanding their ecology (Kremen 2005). Substantial progress has been made in understanding regulating and provisioning services, including the development of production functions that link biophysical processes to ecosystem service supply and allow ecosystem services to be mapped and evaluated at multiple spatial and temporal scales (Daily and Matson 2008; Kareiva et al. 2011). Cultural ecosystem services (the non-material benefits received from nature) are consistently recognized as important, but are often considered difficult to measure and are seldom quantified (Feld et al. 2009; Daniel et al. 2012). Thus, understanding of the supply and dynamics of cultural ecosystem services lags behind that of other ecosystem services.

Cultural ecosystem services, such as ecotourism, nature observation and human well-being, often depend directly upon biodiversity (Naidoo and Adamowicz 2005; Fuller et al. 2007; Mace et al. 2012), but are largely absent from biodiversity-ecosystem service studies (Cardinale et al. 2012, with notable exceptions, see: Quetier et al. 2007; Villamagna et al. 2014). Many cultural ecosystem services rely on seasonally dynamic species. For example, appreciation of fall foliage color depends on seasonal variation in the biotic community (Wood et al. 2013); wildflower viewing depends on flower phenology (Turpie and Joubert 2004), which can vary by species and environmental setting; and wildlife watching varies with seasonal differences in species presence, abundance and behavior (Lambert et al. 2010). Thus, supply of many biodiversity-based ecosystem services is likely shift seasonally. However, ecosystem service studies have tended to use simple indicators and static data sources that ignore the ecology and temporal dynamics of biotic communities (Kremen 2005; Luck et al. 2009). Early studies of ecosystem services used simple models based on land-use proxies to describe the spatial pattern of service provision (Chan et al. 2006; Troy and Wilson 2006). Few ecosystem service studies addressed the contribution of biodiversity to ecosystem services (Kremen 2005). Ecosystem service studies have evolved over time to use empirically-derived and process-based models that consider more detailed spatial and temporal data (e.g. soil, climate, management within land-use types) (e.g., Sharp et al. 2016) but cultural ecosystem service models remain limited with only 17 % including multi-temporal assessments and less than 25 % incorporating spatially explicit information (Hernández-Morcillo et al. 2013). Models of ecosystem services that represent static spatial distributions (Anderson et al. 2009; Raudsepp-Hearne et al. 2010; Holland et al. 2011a) may obscure heterogeneity in ecosystem service supply and simplify relationships between landscape gradients, biodiversity and ecosystem services (Eigenbrod et al. 2010).

Viewing and photographing wildflowers is among the fastest growing forest-based recreation activities in the United States, with over 40 % of adults participating (Cordell 2012), and an exemplar of a cultural ecosystem service that depends directly on biodiversity. Wildflower viewing depends on the presence of wildflower blooms, which are heterogeneous in time and space. Spatial–temporal dynamics of floral resources have strong effects on plant-pollinator interactions (Kremen et al. 2007; Williams and Winfree 2013; Matteson et al. 2013) but consequences of landscape-scale variation in floral resources for cultural ecosystem services are unknown (Lavorel et al. 2011; Quijas et al. 2012). Variation in floral resources may have important impacts for management of nature-based economies (Turpie and Joubert 2004; Sakurai et al. 2011).

Few studies assess spatial–temporal variation in floral resources at the community level and seldom examine flower communities from an anthropogenic perspective. Spatial variation in floral resources can result from distribution patterns of particular species or functional groups responding to climate conditions or local environmental factors such as topography, soils, and disturbance history (Hermy and Verheyen 2007; Jackson et al. 2012; Gornish and Tylianakis 2013) as well as temporal variation in flowering due to climate and seasonality (Fitter and Fitter 2002; Cleland et al. 2007; Crimmins et al. 2008; Aldridge et al. 2011; Holden et al. 2011; Crimmins et al. 2013). Spatial and temporal patterns of floral resources are affected by human modification of the surrounding landscape (Ford et al. 2000; Foley et al. 2005; Tscharntke et al. 2005; Knapp et al. 2012). Increased anthropogenic influence is associated with increases in non-native flora (Kuhman et al. 2010), declines in phylogenetic diversity (Knapp et al. 2012), and advanced onset of flowering (Neil et al. 2010) while changes in forest cover and structure are associated with shifts in understory plant communities including reduced species richness, cover and abundance of native herbs and increased cover of non-native species (Bellemare et al. 2002; Vellend 2005; Kuhman et al. 2011).

We sampled wildflower communities across topoedaphic, climatic, and land use gradients in the southern Appalachian Mountains and asked: (1) How do floral resources (wildflower species richness, abundance, timing, and presence of charismatic species) change over the growing season, and what factors explain this variation? (2) How do projected hotspots of floral resources vary over space and time? (3) How do spatial shifts in floral resource affect potential public access to cultural ecosystem service supply? We hypothesized that topoedaphic conditions would have strong effects on all floral resources and that flower species richness would decline with increased anthropogenic influence.

Methods

Study area

The French Broad River Basin (FBRB), located within the Southern Blue Ridge physiographic region in the southern Appalachian Mountains, covers an area of 7330 km^2. Elevation ranges from 300 to 2100 m, and the climate is characterized by mild winters (−2 °C), warm summers (23 °C) and abundant precipitation (1020–2440 mm annually) (Thornton et al. 2012). Soils are generally Inceptisols, with some Ultisols (Soil Survey Staff 2013). The region is characterized by high biodiversity and ecotourism is popular (SAMAB 1996). The regional economy changed in the last century from resource extraction (e.g., timber) and agricultural production to a nature-based, amenity-driven economy, leading to altered patterns of land use and land cover (Wear and Bolstad 1998; Turner et al. 2003; Gragson and Bolstad 2006). North Carolina tourism office estimates that tourism's impact increased from $269 million in 1991 to $901 million in 2013 in one urban center in the region, with combined visitor expenditures for 2014 over $1330 million for the FBRB (Strom and Kerstein 2015, VisitNC 2016). While no data specifically report dollars generated by ecotourism, overnight visitors to the North Carolina Mountain Region reported participating in rural sightseeing (26 %), visiting state/national parks (23 %), wildlife viewing (14 %), hiking/backpacking (10 %), nature/ecotouring (9 %), other nature (8 %), and birdwatching (4 %) during 2014 (VisitNC 2016). From 1976 to 2006, human population increased by 48 % (Vogler et al. 2010), accompanied by increased exurban, low-density housing development and increased forest land cover. The FBRB is dominated by forest (75 %), mainly secondary growth. Forest types consist of spruce-fir (*Picea abies*) and northern hardwoods at high elevations, mixed hardwood species at lower elevations, and mixed mesophytic forests on lower slopes and coves (SAMAB 1996). Agriculture comprises 12 % of the landscape, over 70 % of which is managed as meadow or pasture. Urban areas constitute 12 % of the landscape and the remainder consists of shrubland, water, or barren land (all <1 %) (Homer et al. 2012). Recent stakeholder interviews indicate that area residents strongly value biodiversity and are concerned for the futures of ecosystem services, particularly cultural ecosystem services (GroWNC 2013).

Wildflower surveys

Site selection

Wildflower communities were surveyed at 63 sites located on public and private property (SM Figure S1). We stratified the study area by elevation, building density, and land use. Sites were located in forested areas (n = 51) or open fields (e.g., pastures or low-intensity hay fields, n = 12) and within 150 m of trails or roads to characterize floral resources likely to be visible to people. Sites on public property were randomly located using the Sampling Design tool for ArcGIS 10.0. Private property site selection followed an iterative process. First, we invited property owners to participate through messages to area landowner networks as well as personal and professional networks. Second, each property was evaluated relative to our stratification scheme and visited to determine site-suitability (e.g. accessibility, areas without active cultivation). Study sites were randomly located on the selected properties using digitized maps of the property boundaries and the Sampling Design tool for ArcGIS 10.0.

Survey methods

A 50 × 2 m belt transect was established at each site. We avoided areas of active cultivation or horticulture. Sites were visited at least once every 3 weeks from April 1 to August 8, 2014. During each visit, we tallied the number of flowering individuals, identified each flowering individual to species, and estimated percent cover of flowers along the transect. We classified each species using charismatic species status. Charismatic species were determined by conducting a search of tourism websites using the terms "western North Carolina", "southern Appalachian Mountains", or "Asheville, North Carolina" and listing all flowering species mentioned by name or appearing in photographs on those websites; species that appeared on ≥40 % of tourism websites were considered charismatic (SM Table S1). Data post-processing included grouping some of the flower species to genus based on similarity in appearance and potential misidentification. See Supplemental Materials for a complete list of species observed in bloom and grouped species (SM Table S2). All analyses used the grouped list.

Covariate data

Each site was assigned a site type (i.e., forest = 1 or open = 2). Environmental variables were extracted from GIS data. Elevation, slope, aspect, and topographic position index (TPI) were calculated from the National Elevation Dataset 30 m digital elevation model (Gesch et al. 2002). The TPI describes the relative position of a site given nearby terrain; negative values indicate that a site is below the average elevation of its neighborhood (e.g., valleys and coves) whereas positive values indicate it is above the average elevation of its neighborhood (e.g., ridges and hilltops). We converted aspect to a relative moisture index ranging from 1 to 16, with SSW (1) as the driest aspect and NNE (16) as the wettest (Day and Monk 1974). Soil percent organic matter was extracted from the SSURGO soil database (Soil Survey Staff 2013).

Climate data for 2014 were calculated from the Daymet dataset (Thornton et al. 2012) which provides 1 km gridded estimates of daily weather for North America, including daily minimum and maximum temperature, precipitation occurrence and amount. We used cumulative growing degree days (GDD) and precipitation accumulated to the end of our sampling season to characterize climate for the full sampling period.

Building density (building units per hectare) was quantified by tallying all buildings located within 100 m of each study site. We used centroids of digitized building footprints obtained from county government GIS offices to locate buildings. We quantified vegetation structure and forest canopy cover from light detection and ranging data. See Supplementary Methods for more details.

Data analysis

Analysis of observed floral resources

Nine response variables were calculated and represented three components of floral resources (i.e., flower species richness, flower abundance, and charismatic species richness). Flower species richness and flower abundance were analyzed at two temporal scales (i.e., full growing season and subseason).

Flower species richness

To account for differences in observed species richness due to survey effort (e.g., weekly sampling versus tri-weekly sampling), we calculated flower species richness using species accumulation curves and the *vegan* package in R (Oksanen et al. 2015). We calculated flower species richness for the full 18-week season and for early spring, late spring, and summer (three 6-week subseasons).

Flower abundance

Peak bloom abundance, i.e., the maximum abundance during the full season, and subseason flower abundance, i.e., mean abundance within early spring, late spring, and summer, were calculated for each site.

Charismatic species

We calculated the proportional presence of charismatic species at each site as the number of charismatic species observed at that site divided by the total number of species observed at that site.

Factors influencing species richness, flower abundance, and flower timing were analyzed using Poisson regression and AICc model selection (*glm* function in package *lme4* for R; Bates et al. 2015). Binomial regression and AICc model selection were used to analyze the proportional presence of charismatic species. All covariates were standardized to mean = 0 and variance = 1, to directly compare regression coefficients as a measure of effect size. Candidate models included quadratic terms for building density, soil organic matter, and precipitation as well as interaction terms (GDD × building density; GDD × percent tree cover). For each response variable, the candidate suite of models included a full model with all covariates, single models for each predictor, and step-wise combinations of multi-variable models from the full model. Models were ranked according to second-order Akaike's information criterion (AICc) (Burnham and Anderson 2002). We inspected all models within ΔAICc < 2 of the top-ranked model. Results and coefficient estimates from all competing models within ΔAICc < 2 of the top model are presented in the Supplemental Information (Tables S4–S7). Below, we report covariate relationships with respect to the relative strength and direction of each covariate on the response variable across all competing models. See supplementary materials for more details on data analysis.

Analysis of projected landscape patterns of wildflower resources

We created maps of projected wildflower resources using the *predict* function in the *raster* package for R (Hijmans and van Etten 2015) and predicted values from best-fitting models identified in the analysis above. For response variables with competing top models, we first mapped the predicted value from each of the competing top models. Final maps were created by calculating the weighted-average of the mapped top model predictions, using the corresponding AICc model weights, rather than using model-averaged coefficients (Grueber et al. 2011; Cade 2015). All input layers were standardized to z-scores based on the mean and variance of the sampled dataset (n = 63) and referenced to the same UTM projection (NAD 1983 UTM 17N) and 30 m grid cell. For more detail on preparation of input data layers, see Supplemental Material. For maps of the standard error of each predicted response, see supplemental material (SM Figure S2).

Hotspots of individual floral resources were identified for each response variable by calculating the upper 20th percentile of projected values for 30 m grid cells (SM Fig. 3). Hotspots for multiple floral resources were identified by overlaying maps of the upper 20th percentile of each response variable (sensu Qiu and Turner 2013). We identified hotspots at two temporal scales: full season and subseason (early spring, late spring, and summer) and analyzed temporal consistency of hotspots by assessing spatial concordance of hotspots among subseasons.

Analysis of wildflower viewing accessibility

We compared maps of projected floral resources to maps of public access to examine how access to floral resources changed over time. We identified public access as any publicly owned lands (e.g. federal and state-owned forests and parks) as well as locations within 30 m of public-use trails such as greenways and bike trails (Table S3). For each time period and each floral resource, we calculated the area overlap between hotspots and public access.

Results

Observed floral resources

Flower species richness

Two hundred thirty flower species were recorded in bloom across all study sites from April 1 to August 8, 2014 (see Table S2 for full list); this list was reduced to 173 flower species for analysis. Sites varied in the number of species recorded in flower throughout the season (April–August) with total flower species richness ranging from 2 to 34 species ($\bar{x} = 12 \pm 0.88$) per site. Mean flower species richness among all sites was similar through the growing season, but flower species richness at each site varied by subseason (Fig. 1).

Total flower species richness was higher at sites with lower precipitation, tree cover and building densities (Table S4). There were strong non-linear effects of soil organic matter (positive quadratic effect) on flower species richness; richness declined at intermediate soil organic matter levels and

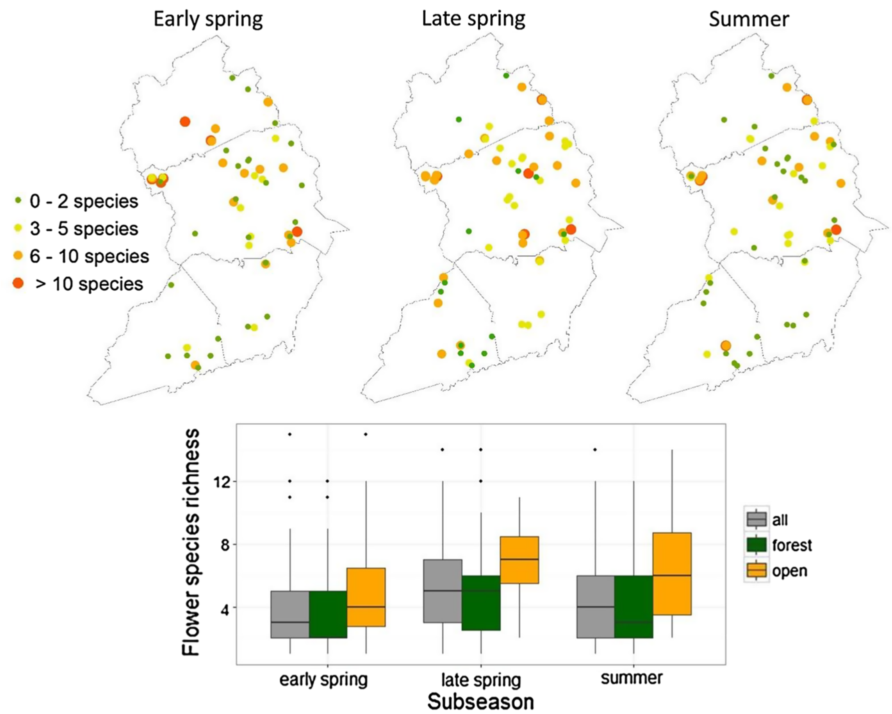

Fig. 1 Observed flower species richness at study sites in the French Broad River Basin during early spring, late spring, and summer 2014

increased at higher levels of organic matter. Flower species richness was also influenced by the interaction of GDD with percent cover of trees and building density; at warmer sites, where GDD were higher, the negative effects of tree cover were dampened whereas the conditional effect of building density was more negative as GDD increased.

The relative effect of topoedaphic variables, climate, local vegetation, and building density on flower species richness varied among subseasons (Table S5). Climate, soil organic matter and building density were most important for flower species richness during early spring, with cumulative precipitation exerting the most influence on species richness. The effect of GDD on subseason flower species richness was positive in early spring as days warmed and species began to bloom before leaf out, but changed to negative in late spring as higher elevation sites had more species in bloom and the forest canopy closed. Building density was important for flower species richness with strong nonlinear effects in early spring, wherein the highest richness occurred at intermediate levels of building density, and strong negative effects in late spring and summer. Soil organic matter affected flower species richness in all seasons.

Flower abundance

Observed peak bloom abundance ranged from 8 to 1828 flowers per site ($\bar{x} = 194 \pm 44.1$). Peak bloom abundances at open sites ($\bar{x} = 659 \pm 170$) were substantially higher than in forested sites ($\bar{x} = 84 \pm 14.7$) and site type was most important for explaining peak bloom abundance. Topoedaphic conditions had significant effects on peak bloom abundance, with positive effects of soil organic matter, topographic moisture index, and slope (Table S6). The negative effects of TPI indicated that higher peak bloom abundances were found at lower topographic positions relative to the surrounding terrain. Climate affected peak bloom abundance with strong non-linear effects of precipitation. Building density had a small positive effect on peak bloom abundance.

Mean flower abundance changed through the season and differed between open and forested sites (Fig. 2). Factors affecting flower abundance varied in their relative importance and direction of effect across subseasons. Site type was the most important factor during all subseasons, with higher flower abundances occurring at open sites. Climate and topoedaphic conditions had the greatest effects in early and late

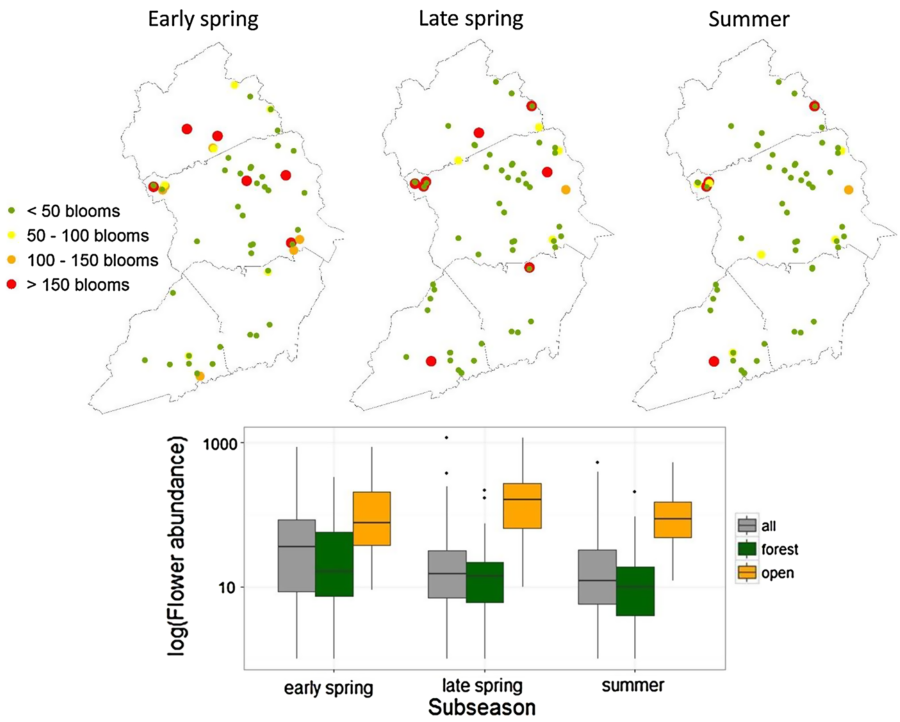

Fig. 2 Observed flower abundance at study sites in the French Broad River Basin during three subseasons between April and August 2014

spring while GDD and building density had the strongest (negative) effects on summer flower abundance.

Topoedaphic factors varied in their effects on flower abundance over the season. Topographic wetness index had strong positive effects in early spring, but lower relative and negative effects on late spring and summer flower abundance. Slope had positive effects in early and late spring but negative effects in summer. TPI had negative effects in early and late spring, but no effect on summer flower abundance. Soil organic matter was negatively related to flower abundance, with strong nonlinear (positive quadratic) effects, in all subseasons.

Growing degree days had a strong negative effect on flower abundance in all subseasons, but had the strongest relative effect during the late spring where it was the second most important factor explaining flower abundance. The effect of precipitation on flower abundance changed over the season, with negative quadratic effects in early and late spring and positive quadratic effects during summer.

Building density had strong negative effects on summer flower abundance and was among the most important factors explaining flower abundance during summer. The effect of building density on early spring flower abundance was positive and was of lower relative importance than climate and topoedaphic variables. In all subseasons, significant interactions indicate that surrounding building density effects were modulated by the effect of GDD.

Charismatic species

Charismatic species were present at all sites, representing 5 to 100 % of the total flower species richness per site ($\bar{x} = 35$ %). Competing top models predicting the proportion of total flower species richness comprised of charismatic species all included strong effects of topography and precipitation (Table S7). Greater proportions of charismatic species were found at moister sites (higher topographic wetness index) in valley or cove locations (lower TPI) with higher precipitation. However, these models explained a relatively small proportion (pseudo-$R^2 = 0.25$ to 0.30) of variance in the data.

Projected landscape patterns of wildflower resources

Projected floral resources varied substantially across the landscape and through the season and were spatially autocorrelated (all Moran's $I > 0.72$, $p < 0.001$). Hotspots of floral resources (the top 20th percentile of each component of floral resources), were not often spatially co-located or temporally consistent through the season (Fig. 3). Hotspots of overall flower species richness were few in number and relatively small in size (patch density = 2.8 km^{-1}; area-weighted mean patch size = 0.15 ha). Hotspots of flower species richness varied in number and size across subseasons and were largest during early spring and most numerous during late spring (Table 1). Hotspots of peak bloom abundance were more numerous than overall flower species richness hotspots but smaller in size (patch density = 13.6 km^{-1}; area-weighted mean patch size = 0.04 ha). Hotspots of flower abundance were largest during summer and most numerous during the early spring (Table 1). Spatial concordance of hot spots of flower species richness and flower abundance covered 5 % of the landscape in early spring, 10 % in late spring and 7 % in summer, and areas of concordance shifted with subseason (Fig. 4a–c).

Four percent of the landscape was designated to be flower richness coldspots; locations that consistently had low values of flower species richness (e.g., bottom 20th percentile) across all three time periods. Conversely, 6 % of the landscape consistently was in the top 20th percentile of flower species richness in early spring, late spring, and summer, e.g. wildflower richness hotspots (Fig. 4d). Coldspots of wildflower abundance occupied 2 % of the landscape while consistent wildflower abundance hotspots comprised 10 % of the landscape (Fig. 4e).

Accessibility of wildflower viewing

Up to 30 % of the landscape within the study area is publicly accessible for wildflower viewing. The accessibility of wildflower richness hotspots fluctuated through the seasons, with the highest proportion (37 %) accessible during the late spring (Fig. 5). Wildflower abundance hotspots in late spring and summer were often located on privately-owned land, in pastures or fields. However, increases in blooming during July and early August led to an increase in the accessibility of abundance hotspots throughout the early spring to summer season: 25 % accessible in early spring, 30 % during the late spring, and 32 % in the summer. Finally, publicly accessible land tended to have a larger proportion of charismatic species (e.g., >45 % of the total flower species richness at those locations) than private lands.

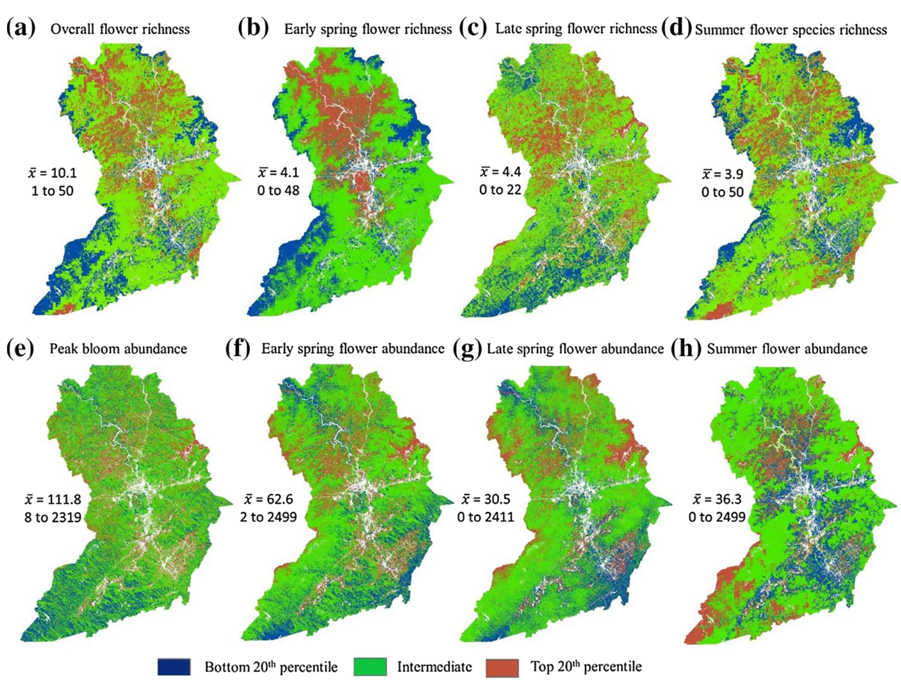

Fig. 3 Projected distribution of (**a**) overall flower species richness, (**b**) early spring richness, (**c**) late spring richness, (**d**) summer richness, (**e**) peak bloom abundance, (**f**) early spring abundance, (**g**) late spring abundance, and (**h**) summer abundance for the French Broad River Basin. Projections based on AICc-selected models from sites (n = 63) sampled during April to August 2014

Table 1 Summary of the number and size of patches of projected hotspots of floral resources in the French Broad River Basin, North Carolina

Projected floral resource	Threshold used to define hotspot	Number of hotspot patches	Hotspot patch density (km^{-1})	Area-weighted mean patch size (ha)
Flower species richness				
Total (overall)	>13 Species	12,187	2.76	0.15
Early spring	>6 Species	15,501	3.49	1.60
Late spring	>5 Species	27,432	6.20	0.21
Summer	>5 Species	14,230	3.22	0.07
Flower abundance				
Peak bloom	>810 Flowers	58,717	13.56	0.04
Early spring	>470 Flowers	28,231	8.69	0.13
Late spring	>410 Flowers	39,148	8.86	0.17
Summer	>330 Flowers	31,888	7.23	0.37

Results are reported for the entire study period and by season

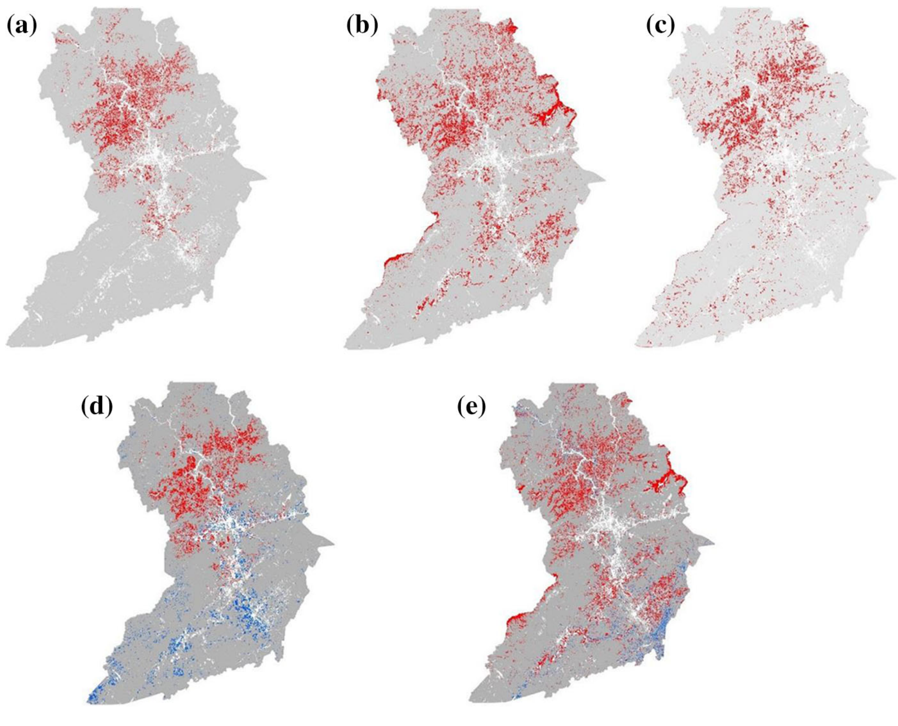

Fig. 4 Spatial distribution of combined hotspots of flower species richness and abundance during (**a**) early spring, (**b**) late spring, (**c**) summer as well as the location of consistent hotspots (*red*) and coldspots (*blue*) of (**d**) flower species richness and (**e**) flower abundance across three subseasons

Discussion

Cultural ecosystem services, important but less well-studied than other ecosystem services, often depend on biotic communities that shift in response to changing environmental conditions and resources. However, temporal dynamics of biotic communities are rarely included in ecosystem service models. Wildflower

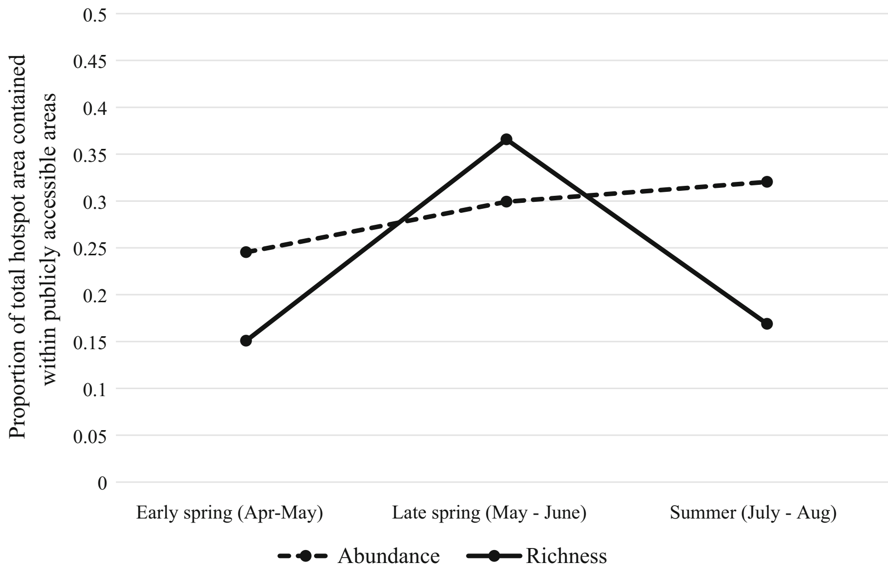

Fig. 5 Projected seasonal change in the proportion of floral resource hotspots within publicly accessible areas in the French Broad River Basin

viewing, an important cultural ecosystem service that contributes to the ecotourism economy in the Southern Appalachians (Watson et al. 1992), depends on the presence and abundance of seasonally-dynamic floral resources. We analyzed factors affecting the richness, abundance, and timing of flowers, mapped the projected supply of floral resources, and identified hotspots of cultural ecosystem service supply. Incorporating temporal dynamics of wildflower blooms identified complex seasonal relationships with environmental variables and uncovered seasonal variation in the supply and accessibility of potential ecosystem services.

Ecosystem services provided by wildflower communities are known to vary with land use/land cover and management intensity (Quetier et al. 2007; Fontana et al. 2014). Floral resources in the Southern Appalachians varied with land use, climate and topoedaphic conditions, and seasonal change in floral resources influenced projected landscape patterns of ecosystem services. The effect of climate on wildflower blooms varied throughout the season, reflecting shifts from lower to higher elevations. Peak bloom abundances tended to occur earliest on drier, warmer forested sites, which likely reflects understory plant community response to aspect-driven microclimate and light availability prior to canopy closure (Gilliam 2007).

Open sites were associated with increased flower abundances and longer flowering seasons than forested sites, while forested sites were associated with a higher proportion of charismatic species. Increased development on agricultural lands, consistent with projected land-use changes in the Southern Appalachians (Wear 2011) could decrease landscape capacity to provide wildflower viewing. Similarly, the strong negative effects of building density on flower species richness suggest that projected increases in residential development may lead to tradeoffs with floral resources. Maintaining a mixture of natural, semi-natural, and agricultural cover types in a predominantly forested landscape may ensure a high diversity of floral resources across multiple seasons and provide increased opportunities to view wildflowers.

As expected, shifts in floral resources changed the locations of wildflower viewing opportunities throughout the season. Many of the open, private lands are considered visible and accessible from roads and trails throughout the region. Publicly accessible lands provide access to floral resources hotspots (e.g. the top 20th percentile of flower species richness or flower abundance), but only 37 % of the area projected to be flower species richness hotspots were publicly accessible. Public access to flower abundance hotspots was highest during the summer, increasing over the season despite a strong shift to open, private lands in late spring and summer. This pattern is a consequence of many public lands, such as national forests, occurring at higher elevations. As wildflower bloom expands upward in elevation, hotspots in public lands also expand. These shifts, coupled with the high proportion of hotspots on private lands, highlight the potential for both public and private lands to have high cultural ecosystem service value and emphasizes the importance of private lands in maintaining ecosystem services (Schaich and Plieninger 2013).

Interannual variation in wildflower community phenology may also contribute to shifts in cultural ecosystem service supply (Forrest et al. 2010). Our study used data collected within 1 year and focused on identifying shifts in cultural ecosystem service supply resulting from seasonal shifts in wildflowers at a finer temporal resolution. Despite the potential for interannual variation, seasonal shifts in floral resources would still alter wildflower viewing supply and access to cultural ecosystem services. Our study adds to the expanding literature recognizing the need to incorporate temporal variation in ecosystem service assessments to fully describe patterns of ecosystem service supply (Nicholson et al. 2009; Holland et al. 2011b; Blumstein and Thompson 2015).

We provide one of the first examples incorporating temporal variability in biotic communities into a spatial assessment of cultural ecosystem service supply. The models presented in this study focus specifically on wildflower richness and abundance in a montane region of the Southern Appalachians. The study area is dominated by forests, with exurban development occurring under the forest canopy (Turner et al. 2003). Our sampling scheme reflected this forest dominance, with only 10 of our 63 sites located in open fields, which may have limited our power to detect variability among open fields. As with all statistical models, caution should be used before transferring these models to other regions as relationships between covariates may differ.

People interested in wildflower viewing (e.g., users of the ecosystem service) may value different components of floral resources based on their individual preferences, beliefs and expertise (Satz et al. 2013), as has been shown for wildlife viewing (Martin 1997). It is often assumed that species-rich views improve the aesthetic value of landscapes (Marshall and Moonen 2002) and increased flower color diversity may provide high cultural ecosystem service value (Quétier et al. 2009; Lindemann-Matthies et al. 2010). Flower-rich views may also increase aesthetic values of landscapes for some viewers (Junge et al. 2009) whereas others may be primarily interested in seeing specific wildflowers of cultural significance or rare species (Martin 1997). Our approach attaches importance to both diversity and abundance of flowers without asserting that one floral component (e.g. richness, abundance, or charismatic species presence) provides a greater or lesser cultural service value. Such differentiation requires understanding stakeholder preferences for particular wildflower arrangements (Turpie and Joubert 2004) and would allow for more detailed evaluation of how the potential wildflower supply affects actual cultural ecosystem service use.

Cultural ecosystem services are not well understood and have been seldom quantified in ecosystem services literature (Daniel et al. 2012). Often, simple proxies based on land-cover or coarse indicators are used to map cultural ecosystem services, such as mapping the amount of green space (Barthel et al. 2005), trails and other recreational facilities (Raudsepp-Hearne et al. 2010; Lovell and Taylor 2013), or some combination of land cover, local features, and nearby population (Qiu and Turner 2013; van Berkel and Verburg 2014). These simple indicators provide little insight into the capacity of a landscape to supply cultural ecosystem services under varying environmental conditions. Further, cultural ecosystem services are often excluded from analysis thereby inhibiting assessments of cultural services in relation to other services or under alternate management scenarios (Hernández-Morcillo et al. 2013).

Our empirical models accounted for temporal dynamics of a biodiversity-based cultural ecosystem service and identified patterns of cultural ecosystem service supply hotspots otherwise obscured by using simple proxies. Such models that incorporate the underlying ecology of cultural ecosystem services have potential to inform policy makers and managers (Daily et al. 2009) and, especially for services that depend on mobile or seasonal biodiversity (Kremen et al. 2007), should be incorporated in future studies to avoid under- or over-emphasizing the importance of particular landscape elements.

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References

Aldridge G, Inouye DW, Forrest JRK, Barr WA, Miller-Rushing AJ (2011) Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. J Ecol 99:905–913

Anderson BJ, Armsworth PR, Eigenbrod F, Thomas CD, Gillings S, Heinemeyer A, Roy DB, Gaston KJ (2009) Spatial covariance between biodiversity and other ecosystem service priorities. J Appl Ecol 46:888–896

Barthel S, Colding J, Elmqvist T, Folke C (2005) History and local management of a biodiversity-rich, urban cultural landscape. Ecol Soc 10(2):10

Bates D, Maechler M, Bolker B, Walker S (2015) lme4: linear mixed-effects models using S4 classes. R package version 1.1-8. R

Bellemare J, Motzkin G, Foster DR (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. J Biogeogr 29:1401–1420

Blumstein M, Thompson JR (2015) Land-use impacts on the quantity and configuration of ecosystem service provisioning in Massachusetts, USA. J Appl Ecol 52:1009–1019

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Cade BS (2015) Model averaging and muddled multimodel inferences. Ecology 96:2370–2382

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67

Chan KM, Shaw MR, Cameron DR, Underwood EC, Daily GC (2006) Conservation planning for ecosystem services. PLoS Biol 4:e379

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends Ecol Evol 22:357–365

Cordell HK (2012) Outdoor recreation trends and futures: a technical document supporting the Forest Service 2010 RPA assessment

Crimmins TM, Crimmins MA, Bertelsen D, Balmat J (2008) Relationships between alpha diversity of plant species in bloom and climatic variables across an elevation gradient. Int J Biometeorol 52:353–366

Crimmins TM, Crimmins MA, Bertelsen CD (2013) Spring and summer patterns in flowering onset, duration, and constancy across a water-limited gradient. Am J Bot 100:1137–1147

Daily GC, Matson PA (2008) Ecosystem services: from theory to implementation. Proc Natl Acad Sci USA 105:9455–9456

Daily GC, Polasky S, Goldstein J, Kareiva PM, Mooney HA, Pejchar L, Ricketts TH, Salzman J, Shallenberger R (2009) Ecosystem services in decision making: time to deliver. Front Ecol Environ 7:21–28

Daniel TC, Muhar A, Arnberger A, Aznar O, Boyd JW, Chan KMA, Costanza R, Elmqvist T, Flint CG, Gobster PH, Gret-Regamey A, Lave R, Muhar S, Penker M, Ribe RG, Schauppenlehner T, Sikor T, Soloviy I, Spierenburg M, Taczanowska K, Tam J, von der Dunk A (2012) Contributions of cultural services to the ecosystem services agenda. Proc Natl Acad Sci USA 109:8812–8819

Day FP, Monk CD (1974) Vegetation patterns on a southern Appalachian watershed. Ecology 55(5):1064–1074

Eigenbrod F, Armsworth PR, Anderson BJ, Heinemeyer A, Gillings S, Roy DB, Thomas CD, Gaston KJ (2010) Error propagation associated with benefits transfer-based mapping of ecosystem services. Biol Conserv 143:2487–2493

Feld CK, da Silva PM, Sousa JP, de Bello F, Bugter R, Grandin U, Hering D, Lavorel S, Mountford O, Pardo I, Paertel M, Roembke J, Sandin L, Jones KB, Harrison P, Martins da Silva P, Paulo Sousa J, PÃrtel M, RÃmbke J, Bruce Jones KB (2009) Indicators of biodiversity and ecosystem services: a synthesis across ecosystems and spatial scales. Oikos 118:1862–1871

Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. Science 296:1689–1691

Foley JA, Defries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309:570–574

Fontana V, Radtke A, Walde J, Tasser E, Wilhalm T, Zerbe S, Tappeiner U (2014) What plant traits tell us: Consequences of land-use change of a traditional agro-forest system on biodiversity and ecosystem service provision. Agric Ecosyst Environ 186:44–53

Ford WM, Odom RH, Hale PE, Chapman BR (2000) Stand-age, stand characteristics, and landform effects on understory herbaceous communities in southern Appalachian cove-hardwoods. Biol Conserv 93:237–246

Forrest J, Inouye DW, Thomson JD (2010) Flowering phenology in subalpine meadows: does climate variation influence community co-flowering patterns? Ecology 91:431–440

Fuller RA, Irvine KN, Devine-Wright P, Warren PH, Gaston KJ (2007) Psychological benefits of greenspace increase with biodiversity. Biol Lett 3:390–394

Gesch D, Oimoen M, Greenlee S, Nelson C, Steuck M, Tyler D (2002) The National Elevation Dataset. Photogramm Eng Remote Sens 68:5–11

Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57:845

Gornish ES, Tylianakis JM (2013) Community shifts under climate change: mechanisms at multiple scales. Am J Bot 100:1422–1434

Gragson TL, Bolstad PV (2006) Land use legacies and the future of Southern Appalachia. Soc Nat Resour 19:175–190

GroWNC (2013) GroWNC regional plan: final report. Asheville

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol 24:699–711

Hermy M, Verheyen K (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. Ecol Res 22:361–371

Hernández-Morcillo M, Plieninger T, Bieling C (2013) An empirical review of cultural ecosystem service indicators. Ecol Indic 29:434–444

Hijmans R, van Etten J (2015) Raster: geographic analysis and modeling with raster data. R Packag. version 2.4-20

Holden ZA, Crimmins MA, Cushman SA, Littell JS (2011) Empirical modeling of spatial and temporal variation in warm season nocturnal air temperatures in two north Idaho mountain ranges, USA. Agric For Meteorol 151:261–269

Holland RA, Eigenbrod F, Armsworth PR, Anderson BJ, Thomas CD, Gaston KJ (2011a) The influence of temporal variation on relationships between ecosystem services. Biodivers Conserv 20:3285–3294

Holland RA, Eigenbrod F, Armsworth PR, Anderson BJ, Thomas CD, Heinemeyer A, Gillings S, Roy DB, Gaston KJ (2011b) Spatial covariation between freshwater and terrestrial ecosystem services. Ecol Appl 21:2034–2048

Homer C, Fry J, Barnes C (2012) The national land cover database. US Geol Surv Fact Sheet 3020(4):1–4

Jackson MM, Turner MG, Pearson SM, Ives AR (2012) Seeing the forest and the trees: multilevel models reveal both species and community patterns. Ecosphere 3:1–16

Junge X, Jacot KA, Bosshard A, Lindemann-Matthies P (2009) Swiss people's attitudes towards field margins for biodiversity conservation. J Nat Conserv 17:150–159

Kareiva P, Tallis H, Ricketts TH, Daily GC, Polasky S (eds) (2011) Natural capital: theory and practice of mapping ecosystem services. Oxford University Press, Oxford

Knapp S, Dinsmore L, Fissore C, Hobbie SE, Jakobsdottir I, Kattge J, King JY, Klotz S, McFadden JP, Cavender-Bares J (2012) Phylogenetic and functional characteristics of household yard floras and their changes along an urbanization gradient. Ecology 93:S83–S98

Kremen C (2005) Managing ecosystem services: what do we need to know about their ecology? Ecol Lett 8:468–479

Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G, Minckley R, Packer L, Potts SG, Roulston T, Steffan-Dewenter I, Vazquez DP, Winfree R, Adams L, Crone EE, Greenleaf SS, Keitt TH, Klein A-M, Regetz J, Ricketts TH, Vázquez DP, Winfree R, Adams L, Crone EE, Greenleaf SS, Keitt TH, Klein A-M, Regetz J, Ricketts TH (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol Lett 10:299–314

Kuhman TR, Pearson SM, Turner MG (2010) Effects of land-use history and the contemporary landscape on non-native plant invasion at local and regional scales in the forest-dominated southern Appalachians. Landscape Ecol 25:1433–1445

Kuhman TR, Pearson SM, Turner MG (2011) Agricultural land-use history increases non-native plant invasion in a southern Appalachian forest a century after abandonment. Can J For Res 41:920–929

Lambert E, Hunter C, Pierce GJ, MacLeod CD (2010) Sustainable whale-watching tourism and climate change: towards a framework of resilience. J Sustain Tour 18:409–427

Lavorel S, Grigulis K, Lamarque P, Colace MP, Garden D, Girel J, Pellet G, Douzet R (2011) Using plant functional traits to understand the landscape distribution of multiple ecosystem services. J Ecol 99:135–147

Lindemann-Matthies P, Junge X, Matthies D (2010) The influence of plant diversity on people's perception and aesthetic appreciation of grassland vegetation. Biol Conserv 143:195–202

Lovell ST, Taylor JR (2013) Supplying urban ecosystem services through multifunctional green infrastructure in the United States. Landscape Ecol 28:1447–1463

Luck GW, Harrington R, Harrison PA, Kremen C, Pam M, Bugter ROB, Dawson TP, De Bello F, Díaz S, Feld CK, Haslett JR, Hering D, Kontogianni A, Lavorel S, Rounsevell M, Samways J, Sandin L, Settele J, Sykes MT, Van Den Hove S, Zobel M, Berry PMAMM, de Bello F, Diaz S, Samways MJ, van den Hove S, Vandewalle M (2009) Quantifying the contribution of organisms to the provision of ecosystem services. Bioscience 59:223–235

Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: a multilayered relationship. Trends Ecol Evol 27:19–26

Marshall EJP, Moonen AC (2002) Field margins in northern Europe: their functions and interactions with agriculture. Agric Ecosyst Environ 89:5–21

Martin SR (1997) Specialization and differences in setting preferences among wildlife viewers. Hum Dimens Wildl 2:1–18

Matteson KC, Grace JB, Minor ES (2013) Direct and indirect effects of land use on floral resources and flower-visiting insects across an urban landscape. Oikos 122:682–694

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: multiscale assessments. Island Press, Washington, DC

Naidoo R, Adamowicz WL (2005) Biodiversity and nature-based tourism at forest reserves in Uganda. Environ Dev Econ 10:159–178

Neil KL, Landrum L, Wu J (2010) Effects of urbanization on flowering phenology in the metropolitan phoenix region of USA: findings from herbarium records. J Arid Environ 74:440–444

Nicholson E, Mace GM, Armsworth PR, Atkinson G, Buckle S, Clements T, Ewers RM, Fa JE, Gardner TA, Gibbons J, Grenyer R, Metcalfe R, Mourato S, Muuls M, Osborn D, Reuman DC, Watson C, Milner-Gulland EJ (2009) Priority research areas for ecosystem services in a changing world. J App Ecol 46:1139–1144

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2015) Vegan: community ecology package. University of Oulu, Oulu

Qiu J, Turner MG (2013) Spatial interactions among ecosystem services in an urbanizing agricultural watershed. Proc Natl Acad Sci USA 110:12149–12154

Quetier F, Lavorel S, Thuiller W, Davies I (2007) Plant-trait-based modeling assessment of ecosystem-service sensitivity to land-use change. Ecol Appl 17:2377–2386

Quétier F, Rivoal F, Marty P, Chazal J, Thuiller W, Lavorel S (2009) Social representations of an alpine grassland landscape and socio-political discourses on rural development. Reg Environ Chang 10:119–130

Quijas S, Jackson LE, Maass M, Schmid B, Raffaelli D, Balvanera P (2012) Plant diversity and generation of ecosystem services at the landscape scale: expert knowledge assessment. J Appl Ecol 49:929–940

Raudsepp-Hearne C, Peterson GD, Bennett EM (2010) Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. Proc Natl Acad Sci USA 107:5242–5247

Sakurai R, Jacobson SK, Kobori H, Primack R, Oka K, Komatsu N, Machida R (2011) Culture and climate change: Japanese cherry blossom festivals and stakeholders' knowledge and attitudes about global climate change. Biol Conserv 144:654–658

SAMAB (1996) The Southern Appalachian Assessment. Terrestrial resources technical report 5. Atlanta

Satz D, Gould RK, Chan KMA, Guerry A, Norton B, Satterfield T, Halpern BS, Levine J, Woodside U, Hannahs N, Basurto X, Klain S (2013) The challenges of incorporating cultural ecosystem services into environmental assessment. Ambio 42:675–684

Schaich H, Plieninger T (2013) Land ownership drives stand structure and carbon storage of deciduous temperate forests. For Ecol Manag 305:146–157

Sharp R, Tallis HT, Ricketts T, Guerry AD, Wood SA, Chaplin-Kramer R, Nelson E, Ennaanay D, Wolny S, Olwero N, Vigerstol K, Pennington D, Mendoza G, Aukema J, Foster J, Forrest J, Cameron D, Arkema K, Lonsdorf K, Kennedy EC, Verutes G, Kim CK, Guannel G, Papenfus M, Toft J, Marsik M, Bernhardt J, Griffin R, Glowinski K, Chaumont N, Perelman A, Lacayo M, Mandle L, Hamel P, Vogl AL, Rogers L, Bierbower W (2016) InVEST User Guide. The Natural Capital Project, Stanford University, University of Minnesota, The Nature Conservancy, and World Wildlife Fund, Minneapolis

Soil Survey Staff (2013) Soil survey geographic (SSURGO) database. http://sdmdataaccess.nrcs.usda.gov

Strom E, Kerstein R (2015) Mountains and muses: tourism development in Asheville, North Carolina. Ann Tour Res 52:134–147

TEEB (2009) The economics of ecosystems and biodiversity (TEEB) for National and International Policy Makers. Econ Ecosyst Biodivers 1–47

Thornton P, Thornton M, Mayer B, Wilhelmi N, Wei Y, Coo R (2012) Daymet: daily surface weather on a 1 km grid for North America, 1980–2012. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge. http://daymet.ornl.gov/

Troy A, Wilson MA (2006) Mapping ecosystem services: practical challenges and opportunities in linking GIS and value transfer. Ecol Econ 60:435–449

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. Ecol Lett 8:857–874

Turner MG, Pearson SM, Bolstad PV, Wear DN (2003) Effects of land-cover change on spatial pattern of forest communities in the Southern Appalachian Mountains (USA). Landsc Ecol 18:449–464

Turpie J, Joubert A (2004) The value of flower tourism on the Bokkeveld Plateau: a botanical hotspot. Dev South Afr 21:645–662

van Berkel DB, Verburg PH (2014) Spatial quantification and valuation of cultural ecosystem services in an agricultural landscape. Ecol Indic 37:163–174

Vellend M (2005) Land-use history and plant performance in populations of *Trillium grandiflorum*. Biol Conserv 124:217–224

Villamagna AM, Angermeier PL, Niazi N (2014) Evaluating opportunities to enhance ecosystem services in public use areas. Ecosyst Serv 7:167–176

Vogler JB, Shoemaker DA, Dorning M, Meentemeyer RK (2010) Mapping historical development patterns and forecasting urban growth in Western North Carolina: 1976–2030. Charlotte, NC

Watson A, Williams D, Roggenbuck J, Daigle J (1992) Visitor characteristics and preferences for three national forest wildernesses in the South. Page Research Paper INT-455

Wear DN (2011) Forecasts of county-level land uses under three future scenarios: a technical document supporting the Forest Service 2010 RPA assessment. USDA Forest Service, Asheville

Wear DN, Bolstad P (1998) Land-use changes in Southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems 1:575–594

Williams NM, Winfree R (2013) Local habitat characteristics but not landscape urbanization drive pollinator visitation and native plant pollination in forest remnants. Biol Conserv 160:10–18

Wood SA, Guerry AD, Silver JM, Lacayo M (2013) Using social media to quantify nature-based tourism and recreation. Sci Rep 3:2976